Small land snails from Northern Australia, I: Species of *Gyliotrachela* Tomlin, 1930 (Mollusca: Pulmonata, Vertiginidae)

Alan Solem

Field Museum of Natural History,
Roosevelt Road at Lake Shore Drive,
Chicago, Illinois 60605 U.S.A.

SUMMARY

The small vertiginid land snail from Chillagoe Caves, Northern Queensland, *Gyliotrachela australis* (Odhner, 1917), is redescribed and refigured. Three new species, *G. catherina* from near Katherine, Northern Territory, *G. ningbingia* from the Ningbing Ranges north of Kununurra, Western Australia, and *G. napierana* from the Napier Range east of Derby, Western Australia, are described. The pattern of conchological variation in *Gyliotrachela* is discussed and the new taxa compared with extralimital forms.

INTRODUCTION

Several extended field surveys in the northern parts of Western Australia and the Northern Territory, primarily by the author and field associates, were aimed at obtaining camaenid land snails for monographic study (Solem, 1979, 1981a, 1981b). Less attention was paid to the micromollusks, but sufficient materials were obtained to provide at least an introductory review of their distribution and affinities. In a series of short papers, of which this is the first, it is proposed to review and illustrate many of these taxa.

This first contribution covers small pupillids with free, extended apertures containing large and complex barriers.

Several small pupillid taxa with reflexed or extended apertures and generally associated with limestone formations, have been collected at scattered localities from the hill country of northern India and southern China, as far east as Chillagoe Caves in Queensland, Australia. Monographed first in the century by Pilsbry (1916-1918: 192-220), they have been most recently comprehensively reviewed by van Benthem Jutting (1950). There is a probably artificial division into four genera (van Benthem Jutting, 1950: 7, table), based upon whether the last whorl is free or adnate, and whether the parietal and angular barriers on the parietal wall of the aperture are separate or fused.

All of the taxa discussed in this paper can be assigned to the genus *Gyliotrachela* Tomlin, 1930 (= *Gyliauchen* Pilsbry, 1917, not Nicoll, 1915, and *Gyliotrachea* Pilsbry, 1931), which is characterized by having the two apertural barriers separate and the last whorl varying from showing a slightly free aperture to a trumpet-like extension. Whether Hypselostoma Benson, 1856, which differs only in having the parietal and angular barriers fused, actually is distinct, is a matter beyond the scope of this paper. Within the general context of the pupillaceans, *Gyliotrachela*, which retains separate angular and parietal barriers, would be considered more generalized than *Hypselostoma* with its fused barriers.*Hypselostoma*

elephas van Bethem Jutting (1950: 23, fig. 12) stands unchallenged in terms of apertural extension, but the growth reversal seen in *Gyliotrachela depressispira* van Benthem Jutting 1949 (van Benthem Jutting, 1950: 27, fig. 15) is an even more remarkable change in shell morphology. I do not consider it possible, at this time, to make any decision as to the relative degree of specialization shown by these genera.

Works subsequent to the summary of van Benthem Jutting (1950) include descriptions of *G. saxicola* van Benthem Jutting (1960) from Kangar, Perlis, Malaya; *G. salpinx* van Benthem Jutting (1961) from near Raub, Pahang, Malaya; and *G. torticollis* van Benthem Jutting (1962) from Cambodia. Berry (1961) demonstrated that there was habitat selection differences between the two species of *Gyliotrachela* found on Bukit Chintamani, Pahang, Malaya, and subsequently (Berry, 1963) described the genital system and pattern of breeding in *G. depressispira* van Benthem Jutting, 1949. Solem (1974: 192, 202-3, figs. 10b, c, e) illustrated and discussed the habitat preference and aestivating position of *G. depressispira*.

The only previous Australian record is the description of *G. australis* (Odhner, 1917), from deposits of supposed Pleistocene age at the Chillagoe Caves in northern Queensland (17 ° 7'S, 144° 30' E).

This paper describes three new species of *Gyliotrachela* from northern Australia: *G. catherina* from near Katherine, Northern Territory: *G. ningbingia* from the Ningbing Ranges north of Kununurra, Western Australia; and *G. napierana* from the Napier Range, east of Derby, Western Australia. New illustrations and a revised diagnosis of *G. australis* are presented for comparison. It is quite probable that additional Australian taxa will be discovered as limestone areas in the northern half of the continent are more thoroughly investigated for molluscs.

ACKNOWLEDGEMENTS

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PATTERNS OF SHELL VARIATIONS

The Australian taxa known to date apparently form a monophyletic unit that shows the same types of variation documented for the Malayan radiation, so ably reviewed by van Benthem Jutting (1950 *et al*). The numer and relative size of apertureal barriers, degree of apertural detachment, extent of apertural reflection, spire angle, and pattern of body whorl sulcus formation are the obvious features enabling species identification. For each of the Australian taxa, essentially equivalent changes can be found in one or another of the Malayan taxa. This does not imply direct descent or relationship to specific taxa, but rather suggests parallel modification of a rather Protean stock.

The obvious correlation with apertural barrier size may prove to be illusory when more taxa are known. Our sampling is as yet too fragmentary for meaningful conclusions. Nevertheless, the nearly occluded aperture found in *G. napierana* (figs. 9, 13), contrasts

with the much more open aperture with reduced number of barriers found in the easternmost species, *G. australis* (fig. 12). The taxa from the intermediate areas, *G.ningbingia* (fig. 10) and *G. catherina* (fig. 11), form a partially graded series. Because of this, it might be argued that subspeciation rather than speciation is involved. Yet the differences in apertural detachment and reflection, plus the changes in body whorl contour are equivalent to those seen among taxa that are sympatric in Malaya (see van Benthem Jutting, 1950, 1961, Tweedie, 1961). Up to three species of *Gyliotrachela* have been taken on the same small limestone hill in Malaya. These sympatric taxa show the same degree of morphologic difference documented here for the allopatric Australian taxa. Since the many populations sampled in the Ningbing area, although differing slightly in size, agree in basic shell structure, I am confident that these are valid species rather than geographic variants.

Use of the scanning electron microscope (hereafter SEM) has permitted providing more detailed illustrations of shell features than could be attempted by previous workers, and also to include some data on the basic shell microstructure and microarmature on the apertural barrier.

All of the Australian species agree in having the same basic sculptural elements. Study of Malayan material in Field Museum of Natural History confirms that the same patterns are present in Malayan and Indonesian species. The apical sculpture (fig. 14-15) consists of raised polygonal ridges occasionally lifted into minor peaks. These shift near the end of the first whorl into a less regular pattern (figs. 14, 16) that by the body whorl has become a series of almost regularly spaced spiral ridges (fig. 17). This latter structure is what van Benthem Jutting (1961: 47) referred to as "spiral striation". SEM examination shows that all of the above structures are raised calcareous crystals (fig. 16).

The larger apertural barriers are typical of small land snails in that there is a complex microstructure on their upper edges (fig. 18-19) Solem (1972) gave a general survey of their occurrence, illustated a number of the basic types, and presented data as to their possible functional significance in terms of both protection from predation and as an aid to extension of the body from a retracted position. Solem and Lebryk (1976) demonstrated a positive correlation between size of micro-barriers and degree of apertural narrowing by the main barriers, those snails with narrowed apertures having proportionately much larger microprojections than were found in those taxa where the aperture was more open. The same trend holds in *Gyliotrachela*, where the microprojections are very large and numerous in *G. napierana* (figs. 18-19), and smallest in *G. australis*. The form of the microprojection is most similar to that found in *Vertigo morsei* Sterki, 1894 (Solem and Lebryk, 1976, figs. 27-29). These microprojections appear to be amplifications of the basic barrier crystal surface, rather than major additive elements.

Features of general shell shape and body whorl contour do not show geographically correlated variation within Australia. The degree of apertural reflection is greatest in *G. napierana* and *G. australis*, least in *G. catherina*. Apertural detachment is greatest in *G. ningbingia* (fig. 4). Development of a subperipheral sulcus is very great in both *G. australis* (fig. 7) and *G. napierana* (fig. 1), but almost totally absent in *G. catherina* (fig. 5).

SYSTEMATIC REVIEW

All adults were measured with an ocular micrometer and ratios calculated. Means and standard errors of the mean were calculated in micrometer units and then converted into millimeters. *Gyliotrachela* is not especially suitable for statistical analysis of size and shape variations using standard measurements, since the degree of lip flare, "trumpet" extension, and apertural reflection materially affect height and diameter. Thus the size and shape variation reported below is only a rough measure of such differences, but better than verbal description. Measurements of lip flare, trumpet length, apertural inclination would be of value, but at our current level of knowledge, seem unnecessary for species descriptions.

Measurements are summarized in Table 1. The four species are nearly identical in diameter, but show noticeable differences in whorl count and height, which alter the H/D ratios. Variation within species considerably masks the minor mean differences, and

factors of shape, aperture, and whorl contour are better guides to species identity. No key is provided, since any collections from new areas can be expected to yield additional taxa.

Gyliotrachela napierana, n. sp.

Figs. 1, 2, 9, 13

Diagnosis: A species of *Gyliotrachela* with moderate (fig. 1) development of a subperipheral sulcus and strong upward reflection of the aperture. Apertural barriers (figs. 9, 13) very large, long, grossly narrowing opening, full set of accessory barriers present. Other Australian species have either no upward lip reflection, much reduced to absent subperipheral sulcus, and smaller barriers with loss of accessory barriers (*G. ningbingia, G. catherina,* figs. 3, 5, 10, 11) or an even stronger subperipheral sulcus, weak upward reflection of the aperture, but complete loss of the accessory barriers (*G. australis,* figs. 7, 8, 12). The nearest extralimital species, *G. everetti* (E. A. Smith, 1896) from Kalao, Indonesia (FMNH 48812, FMNH 72487) and *G. dohertyi* (Fulton, 1899) from the Tenimber Islands, Indonesia (FMNH 48826) have fewer and smaller barriers, a longer trumpet extension of the lip, no upward reflection of the aperture, gross strengthening of the subperipheral sulcus, and a large umbilical keel.

Description: Shell small, diameter 2.30-3.22mm (mean 2.88mm), with 4 to 4½ (mean 4¼-) whorls. Spire increasing rapidly in width, last quarter of body whorl reflected moderately upward so that lip edge does not extend below whorl base (fig. 1), aperture barely free of penultimate whorl (fig. 2). Height of shell 1.64-2.34 mm (mean 1.97 mm), H/D ratio 0.609-0.855 (mean 0.684). Body whorl with pronounced rounded keel (fig. 1), strong subperipheral sulcus. Aperture strongly flaring, reflected, significantly tilted upward, with only slightly protruded "trumpet". Apertural barriers large (fig. 13), nearly occluding aperture, full compliment of accessory barriers present. Basal and two infrapalatal barriers quite large, former nearly equal in size to parietal and angular barriers. Based on 146 measured adults.

Holotype: WAM 715.79, Station WA-325, 0.6 km south-west of road along north side of Napier Range, 5.9 km north-west of Yammera Gap, Western Australia. "Lennard" 1:100,000 map sheet 3863 — 891:862. Collected by L. Keller and Roger Buick 12 January 1977. Height of shell 1.88 mm, diameter 2.80 mm, H/D ratio 0.671, whorls 4 3/8.

Paratopotypes: WAM 716.79, WAM 717.79, AMS C.117951, FMNH 200514, FMNH 200516, 47 dead adults from the type locality.

Paratypes: Napier Range: NR IX, south-east of Barnett Cave, in small caves and crevices (36 dead adults, WAM 751.76, FMNH 204661, B. Wilson and S. Slack-Smith 30 August 1975); NR IX, near Barnett Cave on south side of range (33 dead adults, WAM 700.79, FMNH 204662 B. Wilson and S. Slack-Smith 30 August 1975); NR VI, leaf litter north-west of Stumpy's Well (7 dead adults, WAM 752.76, FMNH 204659 B. Wilson and S. Slack-Smith 29 August 1975); NR IV, south-west face of range *ca.* 4 km north-west of Barker Gorge (2 dead adults, WAM 702.79, B. Wilson and Shirley Slack-Smith 18 May 1976); WA-312, crevice in rock wall 3.2 km west of Barker Gorge, south side of Napier Range (1 dead adult, FMNH 204664); NR-II-3, *ca.* 2 km north of Barker Gorge, south side (12 dead adults, WAM 703.79, FMNH 204660, B. Wilson and S. Slack-Smith 18 May 1976).

Discussion: Most known localities are from the north-west part of the Napier Range between Barker Gorge and Billy More Yard, with the type locality (WA-325) located between Wombarella and Yammera Gaps to the south-east. Quite probably many additional colonies will be discovered in suitable sheltered niches in the Napier Range. The general absence of records from the more heavily collected portions of the range between Wombarella Gap and Windjana Gorge may indicate restriction to more protected ravine vicinity locations in the northern Napiers. One set (WAM 750.76) is labelled as coming from Tunnel Creek in the far east of the Napiers, but field notes of the collectors suggest that this was mislabelled in processing and actually came from NR V in the northern Napiers. They have not been designated paratypes in view of the uncertain locality.

Specimens from NR-II-3 were a trifle larger in size because the "trumpet lip" was slightly

longer, but equally long extensions were found in other samples.

Gyliotrachela ningbingia, n. sp.

Figs. 3, 4, 10, 14-16, 18, 19

Diagnosis: A species of *Gyliotrachela* with almost complete loss of the subperipheral sulcus, moderate "trumpet" extension of the aperture, little reflection of the body whorl (figs. 3, 4), and significant size reduction of the apertural barriers (fig. 10). *G. catherina* (figs. 5, 6, 11) agrees in body whorl shape and aperture shape, but has lost the columellar and lower infrapalatal barriers, with the others grossly reduced in size. Both *G. napierana* and *G. australis* (Odhner) have strong subperipheral sulci on the body whorl, much more apertural reflection, and very different barrier size and number. None of the Indonesian species appear similar in structure.

Description: Shell small, diameter 2.27-3.03 mm (mean 2.71 mm), with 3 ¾ to 4 ¾ (mean 4 ⅛+) whorls. Spire increasing moderately rapidly in width, last eighth to quarter of body whorl with altered growth pattern, slightly reflected upward on free portion with noticeable "trumpet" extension (fig. 4). Lip edge may (fig. 3) or may not extend below base of body whorl. Height of shell 1.74-2.67 mm (mean 2.14 mm), H/D ratio 0.600-0.986 (mean 0.790). Body whorl with very weakly angled periphery (fig. 3), slight trace of a subperipheral sulcus. Lip (figs. 3, 10) strongly flared. Barriers (fig. 10) noticeably reduced in prominence, occluding a much smaller portion of the aperture, but all present. Based on 78 measured adults.

Holotype: WAM 719.79, Station WA-427, east face of ridge 5.7 km north of No. 8 Bore, north end of Ningbing Range, north of Kununurra, Northern Territory. "Knob Peak" 1:100,000 map sheet 4668 — 544:501. Collected by A. Solem 17 May 1977. Heights of holotype 1.74 mm, diameter 2.47 mm, H/D ratio 0.707, whorls 3 7/8.

Paratopotypes: WAM 720.79, AMS C.117952, FMNH 200495-7, 6 live, 9 dead adults from the type locality.

Paratypes: Ningbing Ranges, north to south geographic sequence: WA-428, small knob 5.4 km north of No. 8 Bore (Knob Peak 4668 — 544:498) (2 dead adults, FMNH 199024); WA-430, isolated knob 5.45 km north of No. 8 Bore (Knob Peak 4668 — 542:498) (1 dead adult, FMNH 199043); WA-426, large hill just south of No. 8 Bore (Knob Peak 4668 — 563:449) (2 dead adults, FMNH 200768, FMNH 200334); WA-434, 2nd peak south of No. 8 Bore (Knob Peak 4668 — 562:439) (2 dead adults, WAM 722.79 FMNH 199053); WA-230, 7 km north of Tanmurray Bore, east face of range (Carlton 4667 — 568:415) 4 live adults, FMNH 200573, WAM 724.79); WA-228, isolated hill 1.5 km north of Tanmurra Creek (Carlton 4667 — 576:367) (4 dead adults, WAM 723.79, FMNH 200569-70); WA-227, 1.5 km north of Tanmurra Bore, east slope of range (Carlton 4667 — 595: 325) (1 dead adult, FMNH 200867); WA-236, 1.8 km north of Four Mile Creek, south end of Ningbing Ranges (Carlton 4667 — 654:096) (3 dead adults, FMNH 199021, FMNH 199059); "Bilarni Cave", 42.5 km north of Kununurra, near Jeremiah Hills (Carlton 4667 — *ca* 732:892) (44 dead adults, WAM 701.79, FMNH 204658).

Discussion: Live specimens were taken on the underside of rocks in shallow talus on relatively open slopes. Individuals were scattered, not clumped as in some *Georissa* occurring sympatrically. No efforts could be made in November 1976 and May 1977 to obtain long series. Camaenids were abundant and diverse in the Ningbings, so these were taken "for record only".

Specimens from the type locality are unusual in being slightly lower in H/D ratio (Table 2), caused by a reduced whorl count.

Gyliotrachela catherina, n. sp.

Figs. 5, 6, 11, 17

Diagnosis: A species of *Gyliotrachela* in which the peripheral angulation and subperipheral sulcus are absent (fig. 5), the aperture is slightly prolonged into a moderate "trumpet", but only slightly reflected upward (fig. 6). Apertural barriers (fig. 11) are greatly

reduced in prominence, normally with the columellar, lower infrapalatal, and suprapalatal barriers absent, and the basal, lower palatal, and upper palatal nearly equal in size. The very different body whorl contour and loss of some barriers easily separate *G. catherina* from any of the other Australian or Indonesian species. Only *G. australis* (Odhner) (fig. 12) goes further in reduction of the apertural barriers.

Description: Shell small, diameter 2.47-3.09 mm (mean 2.89 mm), with 4⅛ to 4¾ (mean 4⅜+) whorls. Spire width increasing slowly (fig. 5), last portion of body whorl very slightly reflected upward, moderately extended to a form a "trumpet " (fig. 6), variably flared. Height of shell 2.07-2.63 mm (mean 2.41 mm), H/D ratio 0.725-0.920 (mean 0.833). Body whorl (fig. 5) almost evenly rounded, slightly flattened above periphery, no trace of a subperipheral sulcus. Size of barriers (fig. 11) grossly reduced, with columellar, lower infrapalatal, and suprapalatal barriers absent, aperture only moderately occluded. Based on 85 measured adults.

Holotype: AMS C.117950, on rocks 19 km south of Katherine along Stuart Highway, Northern Territory. Collected by Vince Kessner 6 January 1979. Height of holotype 2.30 mm, diameter 2.86 mm, H/D ratio 0.805, whorls 4⅜+.

Paratopotypes: AMS C.116598, FMNH 204655, 12 live adults from the type locality.

Paratypes: 1 km west of Stuart Highway, 3 km north of Katherine (4 dead adults, AMS C.116028, Vince Kessner 3 March 1979); in crevices of rocks, 19 km south of Katherine (68 live adults, AMS C.116031, FMNH 204655-6, WAM 721.79, Vince Kessner 13 February 1979).

Discussion: There is significant size differences among the three sampled populations (Table 2), correlating with changes in whorl count, but the shells agree in basic form and structures.

Gyliotrachela australis (Odhner, 1917)

figs. 7, 8, 12

Hypselostoma australis Odhner, 1917, Kungl, Svensk, Vetensk, Handl., 52(16): 98, pl.3, figs. 107-109 — Chillagoe Caves, North Queensland.

Gyliauchen australis (Odhner), Pilsbry, 1921, Manual of Conchology, (2), *26*: 232, pl. 24, figs. 11-13.

Gyliotrachela australis (Odhner), Iredale, 1937, Australian Zool., *8*(4): 305; van Benthem Jutting, 1950, Bull. Raffles Museum, *21*: 44.

Diagnosis: A species of *Gyliotrachela* with an extremely prominent keel and subperipheral sulcus (fig. 7), moderate reflection upward of the aperture, a prominent "trumpet" (fig.8), and with the barriers reduced to five in number with all accessory barriers absent. Of Australian species, only *G. napierana* has an equivalent body whorl contour, but differs dramatically in the larger number and greater size of the apertural barriers (fig. 9). The Indonesian *G. everetti)* (E.A. Smith, 1896) and *G.dohertyi* (Fulton, 1899) agree in reduced number and size of barriers, but have much less apertural upward reflection, narrower spire width, and a prominent umbilical keel that is lacking in the Queensland *G. australis*.

Description: Shell very small, diameter 2.43-3.09 mm (mean 2.74 mm), with 3⅞ to 4⅜ (mean 4⅛) whorls. Spire width increasing rapidly (fig. 7), last part of body whorl moderately reflected upward, lip flared, aperture extended into a short "trumpet" (fig. 8). Height of shell 1.81-2.20 mm (mean 2.03 mm), H/D ratio 0.670-0.831 (mean 0.741). Body whorl with protruded keel (fig. 7), very strong subperipheral sulcus. Apertural barriers low and slender, only parietal, angular, basal, lower palatal and upper palatal present. Based on 24 measured adults.

Material studied: 2nd hole, Chillagoe Caves, Queensland (17° 07', 144 ° 30' E) (24 dead adults, AMS C.54083, WAM 718.79, FMNH 204654).

Discussion: Only a few of the dirt-encrusted sub-fossil specimens could be cleaned to check the apertural barrier features, but no significant variation was noted.

DISCUSSION

While most records of *Gyliotrachela* in Australia are from cave deposits or cave mouth situations, the live material collected by Solem in the Ningbing Range and by Kessner near Katherine show that they live in situations equivalent to the recorded Malayan localities — seepage areas, rock faces, or talus on limestone hills. Collection of living material from such niches will result in smaller samples than sifting cave deposits, but provide better material for further study.

Potentially any limestone hill area in Northern Australia could hold colonies of *Gyliotrachela*, and discovery of many additional species would not be surprising. Their occurrence in the Napier Range, common in the area north-west of Barker Gorge, but so far located only in an unusually shaded and damp area (WA-325) south of Wombarella Gap, suggests a possible water-based limitation of range. Particular attention should be paid to the presence of live, as opposed to "drift", material, and investigations as to the patchiness of the habitat would be worthwhile. Despite extensive collections in the Prince Regent, Drysdale and Mitchell Plateau areas of Western Australia, and near Alice Springs, Northern Terrritory, no trace of *Gyliotrachela* has been found, pointing to a possible limestone association in distribution. Far too little collecting has been done for such negative evidence to be conclusive, but it does suggest intriguing limitations on *Gyliotrachela* range.

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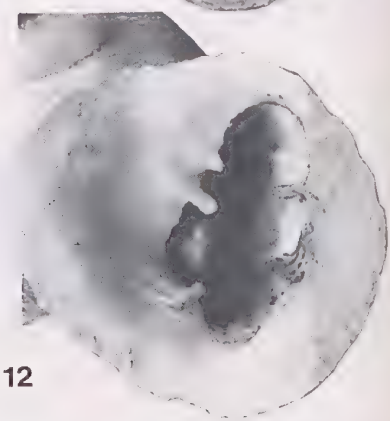
FIGURES 1-6

1-2 *Gyliotrachela napierana* n. sp., WA-325, west of Yammera Gap, Napier Range, Western Australia. Holotpye WAM 715.79, 1. Side views, 23.6 X, 2, Top view, 24.5 X.

3-4. *Gyliotrachela ningbingia* n. sp., WA-427, north of No. 8 Bore, Ningbing Ranges, Western Australia. Holotype. WAM 719.79, 3, Side view, 23.9 X, 4, Top view, 27.3 X.

5-6. *Gyliotrachela catherina* n. sp., 19 km south of Katherine, Northern Territory. Holotype. AMS C. 117950. 5, Top view, 24.9 X, 6, Side view, 24.0 X.



FIGURES 7-12

7-8, 12. *Gyliotrachela australis* (Odhner). Chillagoe Caves, Queensland. FMNH 204654. 7, Side view, 24.1 X, 8, Top view, 24.6 X, 12, detail of aperture, 45.9 X.

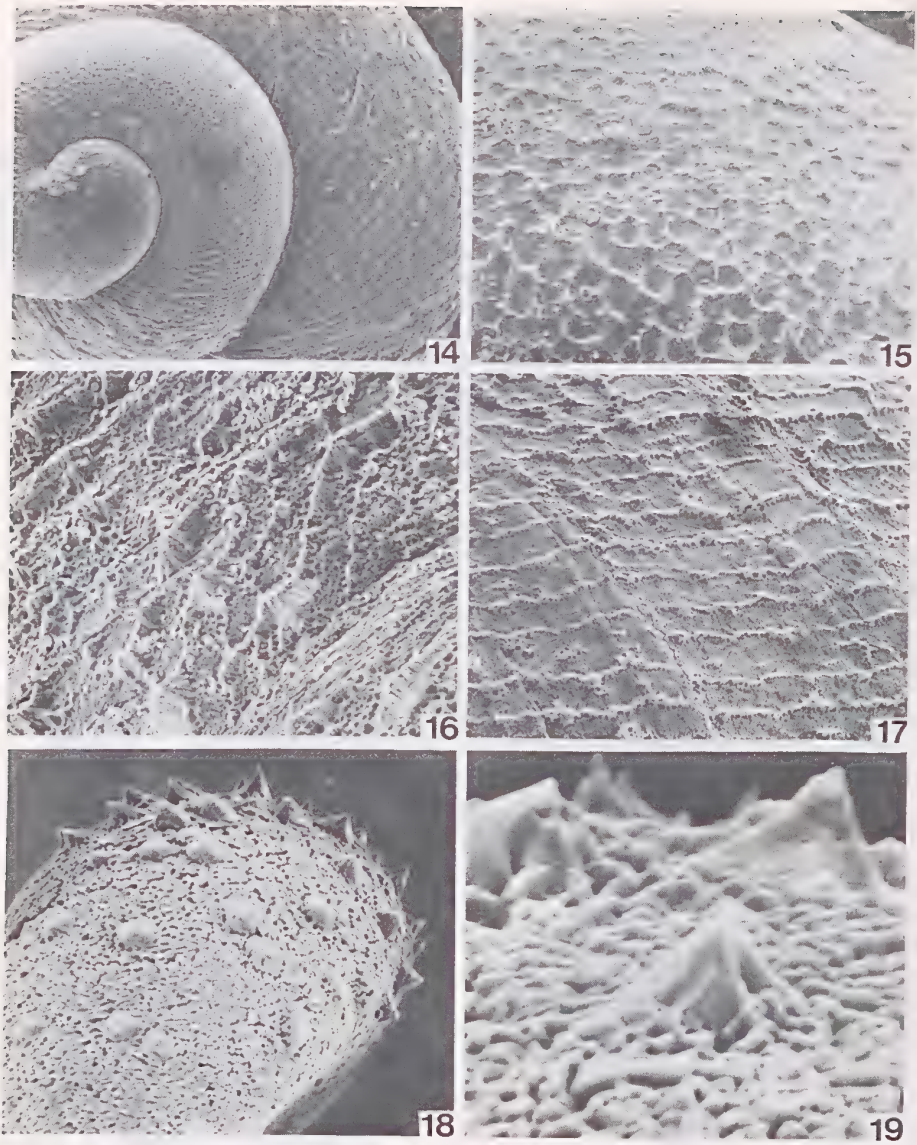
9. *Gyliotrachela napierana* n. sp., WA-325, west of Yammera Gap, Napier Range, Western Australia. Holotype. WAM 715.79. Detail of aperture, 46.6 X.

10. *Gyliotrachela ningbingia* n. sp., WA-427, north of No. 8 Bore, Ningbing Ranges, Western Australia. Holotype. WAM 719.79. Detail of aperture, 46.5 X.

11. *Gyliotrachela catherina* n. sp., 19 km south of Katherine, Northern Territory. Holotype. AMS C.117950. Detail of aperture, 45.9 X.

FIGURE 13

Gyliotrachela napierana n. sp., WA-325, west of Yammera Gap, Napier Range, Western Australia. Paratopotypes. FMNH 200516. Lateral view of major barriers, 215 X.



FIGURES 14-19

14-16. 18-19 *Gyliotrachela ningbingia* n. sp., WA-427, north of No. 8 Bore, Ningbing Ranges, Western Australia. Paratype. FMNH 200496. 14, Apex and early spire, 103 X, 15, Detail of apical sculpture, 522 X, 16, Sculpture on early spire, 527 X, 18, top of parietal barrier, 912 X, 19, Microprojections on parietal barrier top, 4,350 X.

17. *Gyliotrachela catherina* n. sp., 19 km south of Katherine, Northern Territory. Paratype. AMS C.116598. Sculpture on body whorl, 193 X.

Table 1: Range of Variation in Australian *Gyliotrachela*

X and Range of:

Taxon	Measured Adults	Shell Height	Shell Diameter	H/D Ratio	Whorls
G. australis (Odhner)	24	2.03(1.81-2.20)	2.74(2.43-3.09)	0.741(0.670-0.831)	4 1/8 (3 7/8-4 5/8)
G. catherina	85	2.41(2.07-2.63)	2.89(2.47-3.09)	0.833(0.725-0.920)	4 3/8+ (4 1/8-4 3/4)
G. ningbingia	78	2.14(1.74-2.67)	2.71(2.27-3.03)	0.790(0.600-0.986)	4 1/8+ (3 3/4-4 3/4)
G. napierana	146	1.97(1.64-2.34)	2.88(2.40-3.22)	0.684(0.609-0.855)	4 1/4- (4-4 1/2)

Table 2: Local Variation in Australian *Gyliotrachela*

X, SEM, and Range of:

Taxon	Number of Measured Adults	Shell Height in mm	Shell Diameter in mm	H/D Ratio	Whorls
G. napierana					
WA-325, FMNH 200514	18	1.91±0.037 (1.74-2.34)	2.85±0.095 (2.66-2.99)	0.673±0.013 (0.609-0.855)	4 1/4 (4-4 1/2)
WA-325, FMNH 200516	30	1.90±0.019 (1.64-2.11)	2.75±0.023 (2.40-2.93)	0.693±0.006 (0.614-0.747)	4 1/4 (4-4 1/2)
NR IX, WAM 751.76	36	1.98±0.012 (1.84-2.14)	2.91±0.017 (2.70-3.13)	0.682±0.005 (0.621-0.747)	4 1/4- (4-4 1/2)
NR IX, WAM 700.79	33	1.98±0.016 (1.81-2.17)	2.88±0.019 (2.70-3.16)	0.688±0.006 (0.625-0.771)	4 1/8+ (4-4 3/8)
NR II-3, WAM 703.79	12	2.03±0.023 (1.91-2.17)	3.04±0.039 (2.66-3.19)	0.670±0.007 (0.634-0.695)	4 1/4- (4-4 3/8)
G. ningbingia					
WA-327	16	1.94±0.037 (1.74-2.24)	2.72±0.030 (2.47-2.96)	0.717±0.016 (0.600-0.840)	4 1/8 (3 3/4-4 3/8)
"Bilarni Cave" WAM 701.79	44	2.18±0.020 (1.81-2.50)	2.71±0.019 (2.30-2.79)	0.808±0.009 (0.670-0.986)	4 1/8 (3 3/4-4 1/2)

G. catherina					
19 km S, AMS C.116031	68	2.42±0.012 (2.17-2.60)	2.92±0.009 (2.73-3.09)	0.830±0.004 (0.725-0.897)	4 1/2- (4 1/8-4 3/4)
3 km N, AMS C.116028	4	2.10±0.013 (2.07-2.14)	2.52±0.031 (2.47-2.60)	0.837±0.006 (0.823-0.853)	4 1/4- (4 1/8-4 1/4)
19 km S, AMS C.116598	13	2.42±0.031 (2.27-2.63)	2.86±0.021 (2.70-3.03)	0.847±0.011 (0.783-0.920)	4 1/2- (4 1/4-4 3/4)
G. australis					
AMS C.54083	24	2.03±0.022 (1.81-2.20)	2.74±0.033 (2.43-3.09)	0.741±0.008 (0.670-0.831)	4 1/8 (3 7/8-4 3/8)